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EARLY LIFE HISTORY OF *METRIDIA PACIFICA* BRODSKY,
(COPEPODA: CALONIDA) FROM THE SOUTHEASTERN
BERING SEA AND GULF OF ALASKA

By: Alexei I. Pincuck

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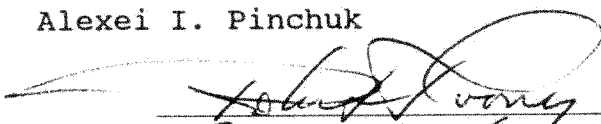
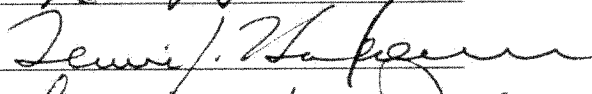
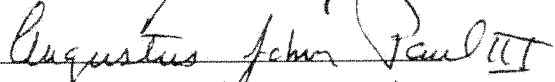
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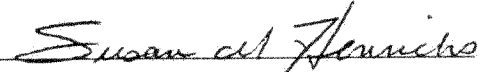
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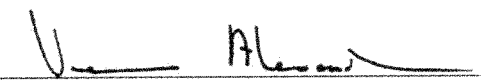
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EARLY LIFE HISTORY OF *METRIDIA PACIFICA* BRODSKY, (COPEPODA:
CALANOIDA) FROM THE SOUTHEASTERN BERING SEA AND GULF OF
ALASKA

A
THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By
Alexei I. Pinchuk

Fairbanks, Alaska

August 1997

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ABSTRACT

The ontogenetic morphological changes of naupliar stages of *Metridia pacifica*, an important prey taxon for larval walleye pollock, were described to facilitate their identification from field samples and to clarify some uncertainties in existing descriptions of co-occurring genera. Clutch sizes and sperm storage potential were determined for females captured from the southeastern Bering Sea and Gulf of Alaska. None of the females produced more than one egg clutch in captivity. The mean clutch size was 12-13 eggs.d⁻¹ for females from both sites and there was no relationship between body size and number of eggs per clutch or egg diameter. Intermolt periods for the egg through N IV stages were 49-120 hours for animals reared at 3°C, 33-69 hours at 6°C and 27-74 hours at 9°C. Growth in length occurred in three slightly different phases, with N I-III, N III-V, and N V-VI each having their own growth pattern. The ratio of body length divided by body width considerably increased from stage N III through N IV. The developmental rate of naupliar stages N I-IV was approximated by an exponential function.

TABLE OF CONTENTS

List of Figures	6
List of Tables	9
Chapter 1. Introduction	10
Chapter 2. Naupliar development of <i>Metridia pacifica</i> (Copepoda: Calanoida) reared in the laboratory	12
Abstract	12
Introduction	12
Methods	13
Results	14
Discussion	25
References Cited	30
Chapter 3. Reproduction of <i>Metridia pacifica</i> and growth of their nauplii in the laboratory	32
Abstract	32
Introduction	33
Methods	33
Results	38
Discussion	46
Acknowledgments	51
References Cited	52
Chapter 4. Discussion	56
Taxonomic clarification	56
Ecological implifications	57

	5
Conclusions	59
References Cited	59

LIST OF FIGURES

Fig. 2.1. *Metridia pacifica*. First to sixth naupliar stages (N I-VI) in ventral view. Appendages omitted for clarity. Arrows indicate new structures as compared with the preceding stage. Scale bar = 100 μm 15

Fig. 2.2. *Metridia pacifica*. Development of naupliar antennules in N I-VI stages. Arrows indicate new structures as compared with the preceding stage. Scale bar = 100 μm .17

Fig. 2.3. *Metridia pacifica*. Development of naupliar antennae in N I-VI stages. Arrows indicate new structures as compared with the preceding stage. Scale bar = 100 μm ... 19

Fig. 2.4. *Metridia pacifica*. Development of naupliar mandibles in N I-VI stages. Arrows indicate new structures as compared with the preceding stage. Scale bar = 100 μm . 21

Fig. 2.5. *Metridia pacifica*. Development of naupliar maxillule (Mx I) and maxilla (Mx II), maxilliped (Mxp), swimming legs 1 (L 1), 2 (L 2). Arrows indicate new structures as compared with the preceding stage. Scale bar = 100 μm 23

Fig. 3.1. Map showing collection sites for *Metridia pacifica*..... 35

Fig. 3.2. Frequency of spawning of isolated female *Metridia pacifica* relying on stored sperm to fertilize the clutch. These females were collected from the Bering Sea (A) and Gulf of Alaska (B) and maintained in the laboratory at 3°C 39

Fig. 3.3. The relationship between the size of *Metridia pacifica* and their eggs. A - female total length (TL) vs. clutch size; B - TL vs. average egg diameter (vertical bars = SD); C - clutch size vs. average egg diameter (vertical bars = SD) 42

Fig. 3.4. Development rates for *Metridia pacifica* naupliar stages N I-IV reared at 3°C, 6°C and 9°C. Symbols are the average times when individuals just entered a stage (horizontal bars = SD) 43

Fig. 3.5. The ratio of body length divided by body width for the naupliar stages of *Metridia pacifica* 44

Fig. 3.6. Duration of the intermolt periods for *Metridia pacifica* naupliar stages N I-III and N VI reared at 3°C, 6°C and 9°C 45

Fig. 3.7. Comparison of average naupliar body length changes in different *Metridia* species 47

Fig. 3.8. Length growth of *Metridia pacifica* naupliar stages N I-IV reared at 3°C, 6°C and 9°C. Data on body length (μm) are logarithmically transformed 48

LIST OF TABLES

Table 2.1. Differences of developmental patterns within the naupliar phase of <i>Metridia pacifica</i> (original data), <i>Metridia lucens</i> (- after Gibbons (1938), - after Ogilvie (1953)) and <i>Neocalanus plumchrus</i> (after Campbell (1934)).	27
Table 2.2. Comparative length measurements (μm) of <i>Metridia</i> nauplii (- original data; - from Paul et al. (1996); - from Ogilvie (1953)) and <i>Neocalanus plumchrus</i> (from Campbell (1934))	29
Table 3.1. Duration of eggs and naupliar stages of <i>Metridia pacifica</i> reared in the laboratory	41

CHAPTER 1

INTRODUCTION.

The Aleutian Basin in the southeastern Bering Sea supports a large walleye pollock fishery (Wespestad, 1993). Recent studies show that larval pollock are very selective as to the type and size of copepod nauplii they eat (Hillgruber et al., 1995). One of the most important prey are naupliar stages of *Metridia pacifica* (Hillgruber et al. 1995; Nakatani, 1995), a common copepod species in the Aleutian Basin (Paul et al., 1996). Our knowledge of the recruitment biology of this copepod is very limited (Batchelder, 1985; Batchelder and Miller, 1989). There are no detailed morphological descriptions of its developmental stages to enable researchers to separate them from numerous co-occurring copepod nauplii. Information on developmental biology, incubation time and growth rates of different stages of *M. pacifica* at different temperatures may clarify temporal variations in larval walleye pollock feeding success. The goal of this thesis is to describe aspects of morphology and basic biology of *M. pacifica* under laboratory conditions. The specific objectives are:

1. Describe the ontogenetic morphological changes of naupliar stages of *M. pacifica*.
2. Examine the capacity for sperm storage by females and egg production rates of *M. pacifica*.

3. Examine the inter-relationships between egg production rate, individual female size, average clutch size and egg diameter.
4. Determine naupliar growth rates over a temperature range of 3° to 9°C.

Chapters 2 and 3 have been prepared as manuscripts for publication. They are written as stand-alone papers with appropriate sections. Chapters 1 and 4 introduce and discuss the results of these manuscripts.

CHAPTER 2

NAUPLIAR DEVELOPMENT OF *METRIDIA PACIFICA* BRODSKY (COPEPODA: CALANOIDA) REARED IN THE LABORATORY¹

ABSTRACT

All 6 naupliar stages of *Metridia pacifica* Brodsky, 1950, are described. Naupliar development is compared within the genus *Metridia* Boeck, 1864, and external morphological characters are discussed with respect to previous studies of co-occurring nauplii of *Calanus*, *Neocalanus* and *Pseudocalanus*. A key to the identification of the naupliar stages is provided.

INTRODUCTION

Knowledge of naupliar morphology is very important for the studies of stage-dependent biological and ecological phenomena. First-feeding walleye pollock (*Theragra chalcogramma* Pallas) in the southeastern Bering Sea are very selective about the species of copepod nauplii and developmental stages that they consume. They prefer *Metridia* nauplii although these stages are relatively rare (Hillgruber et al., 1995). As part of a study of the

¹published as Pinchuk, A.I. 1997. Naupliar development of *Metridia pacifica* (Copepoda: Calanoida) reared in the laboratory. Journal of Crustacean Biology 17: 343-351.

biological and physical variability that influences recruitment of walleye pollock in the southeastern Bering Sea, I describe the naupliar stages of *Metridia pacifica* Brodsky, 1950 and those diagnostic features which facilitate their identification.

METHODS

Adult specimens were sorted from samples collected in the Aleutian Basin of the southeastern Bering Sea and shipped to the Seward Marine Center Laboratory. Females were maintained in separate containers with fresh seawater in a temperature controlled room at 3 °C. These adults were fed *ad libitum* a mixture of autotrophic flagellates (*Isochrysis galbana* and *Tetraselmis suecica*) and the diatom *Chaetoceros calcitrans*. *Artemia* sp., reared for two weeks with the above flagellates, were added to the mixture. During fall, 1995, and winter, 1995-1996, a few females were caught in Resurrection Bay, Gulf of Alaska. They were also kept under the same conditions.

When the eggs hatched, some nauplii were immediately preserved in 10% formalin for later examination. The remaining nauplii were moved into new containers with freshly filtered seawater every fifth day. Specimens and molts of each developmental stage were preserved in 10% formalin. Since I was unsuccessful in rearing these nauplii

beyond stage N IV, specimens of the last two naupliar stages were separated from preserved Bering Sea samples (Paul et al., 1996).

Drawings were made using a *camera lucida*. Two or three specimens per stage were checked for variability. Since no asymmetry of segmentation or setation was observed between sides of paired appendages, only one side of each pair is depicted. The lengths of the nauplii were measured from the anterior margin of the body to the posterior end excluding the caudal setae or spines; body width is provided for the widest part of the naupliar shield. Body measurements were taken from the specimen which is illustrated in the drawings. A light microscope with maximal 1,000 magnification was employed. Abbreviations are: N I-VI = naupliar stages I-VI.

RESULTS

Naupliar Stages of *Metridia pacifica*

The body is illustrated in ventral view (Fig. 2.1). These nauplii are oval, becoming more elongate over the course of development. From stage N III onward, the hind body gradually protrudes caudally from the dorsal shield. There is no visible segmentation of the body through stages N I-IV. The description of each naupliar stage includes only the changes in morphology from the previous stage.

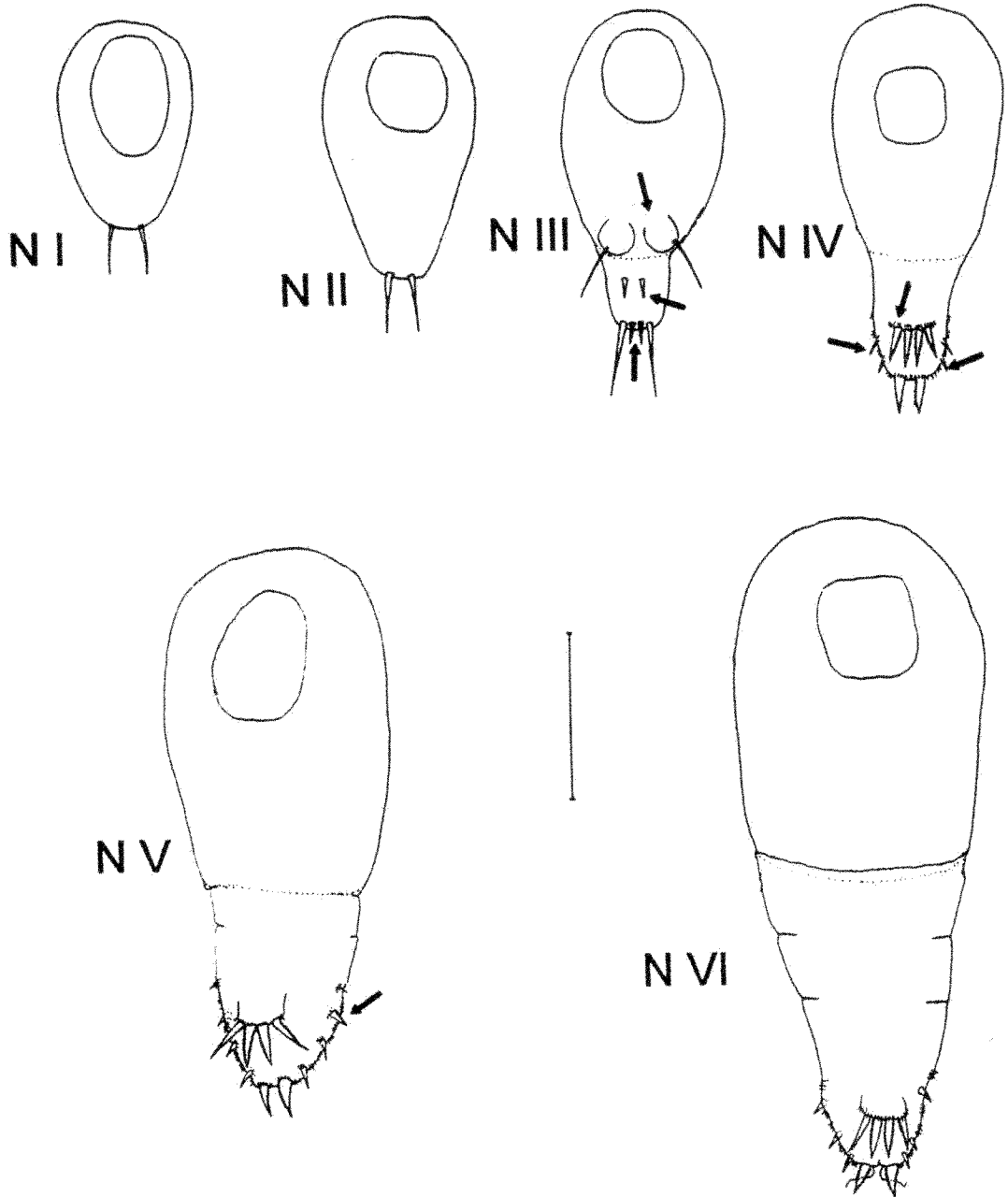


Fig. 2.1. *Metridia pacifica*. First to sixth naupliar stages (N I-VI) in ventral view. Appendages omitted for clarity. Arrows indicate new structures as compared with the preceding stage. Scale bar = 100 μ m.

Nauplius I

The body length of this stage is 150 μm , and its width is 100 μm . The body is broadly oval, rounded at the anterior end, and tapering slightly towards the posterior. The hind body bears a pair of long caudal setae (Fig. 2.1). The labrum is conspicuous ventrally; three pairs of appendages (antennules, antennae and mandibles) are well developed.

The antennule (Fig. 2.2) consists of three segments, and the proximal two segments are devoid of conspicuous armature. The distal third segment bears three terminal setae. The coxa of the antenna is partially separated from the basis and neither are armed (Fig. 2.3). The endopod is two-segmented, partially separated from the basis, and bears two terminal setae. The exopod consists of five segments which are partially separated from the basis; the first to fourth each bear one long seta on their inner margin. The distal segment has two terminal setae. The coxa and basis of the mandible are unarmed (Fig. 2.4). The endopod has one segment and bears two terminal setae. The exopod is four-segmented; the first to third segments each have one seta on their inner margin; the distal segment bears two terminal setae.

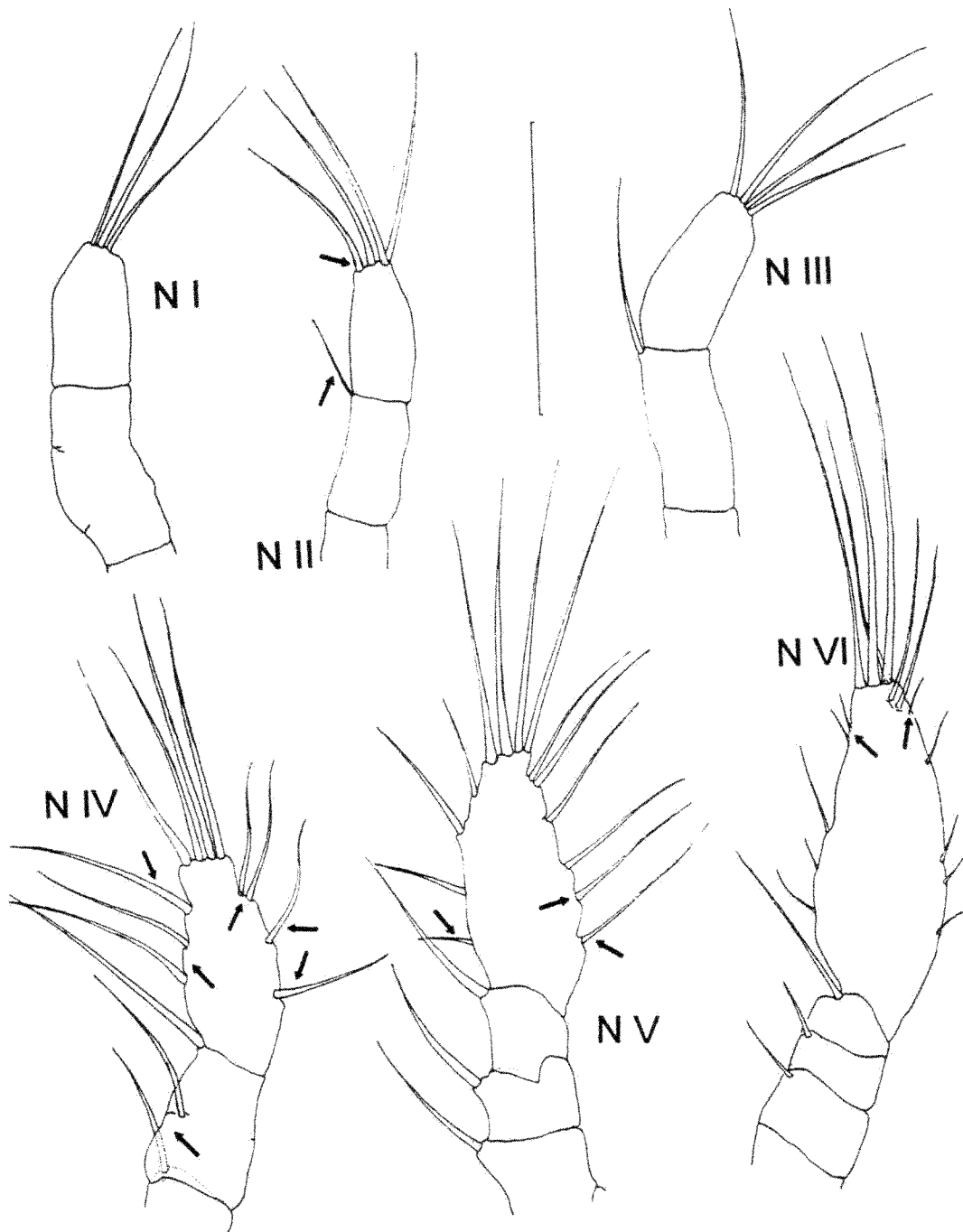


Fig. 2.2. *Metridia pacifica*. Development of naupliar antennules in N I-VI stages. Arrows indicate new structures as compared with the preceding stage. Scale bar = 100 μm .

Nauplius II

The body length is 175 μm , and its width is 100 μm .

Nauplius II differs from N I as follows:

Its body is more tapered posteriorly than N I (Fig. 2.1). The antennule adds a fourth terminal seta and one seta on the ventral margin of the second segment (Fig. 2.2). The endopod of the antenna has three terminal setae (Fig. 2.3). The mandible acquires two spines on the inner margin of the basis and two on the inner margin of the endopod (Fig. 2.4).

Nauplius III

The body length is 200 μm , and its width is 125 μm .

Nauplius III differs from N II as follows:

The anterior part of the body is distinct from the posterior part, which begins posterior to the bud of the maxillule. The hind body bears a pair of caudal setae, a pair of caudal spines and a pair of smaller ventral spines (Fig. 2.1). The coxa of the antenna bears two spines on its inner margin, which do not appear to be articulated with the appendage segment; the basis has one long and one short setae (Fig. 2.3). The endopod adds two spines on the inner margin of the proximal segment and one terminal seta and three setae on the inner margin of the distal segment. The exopod consists of six segments; the proximal segment is not separated from the basis; the third to fifth segment each

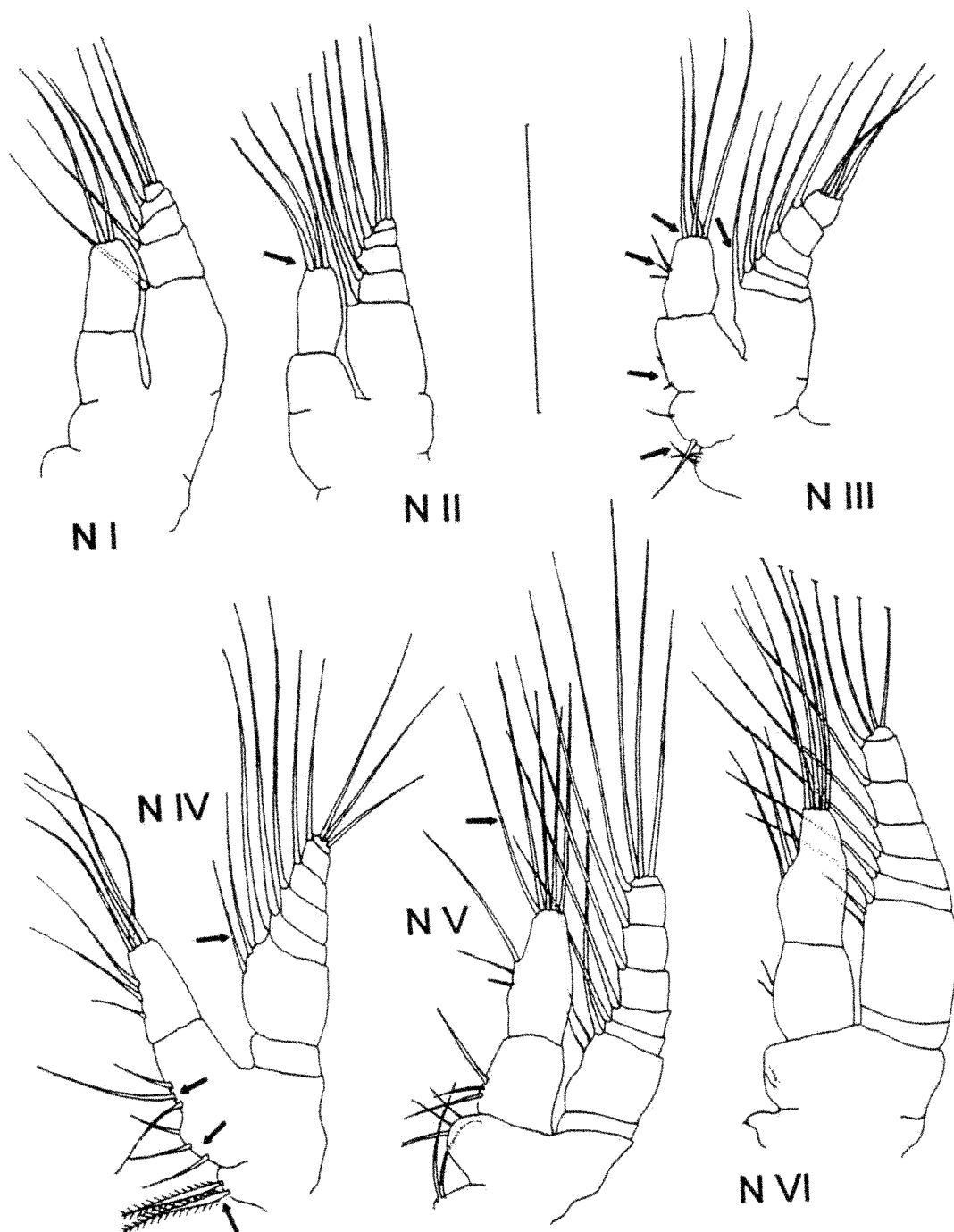


Fig. 2.3. *Metridia pacifica*. Development of naupliar antennae in N I-VI stages. Arrows indicate new structures as compared with the preceding stage. Scale bar = 100 μm .

are armed with one seta on the inner margin; a third seta is added to the distal segment. The coxa of the mandible adds a spine on its inner margin and the inner margin of the basis adds four long and two short setae (Fig. 2.4). The endopod is armed with three setae on its inner margin and three terminal setae. The first segment of the exopod adds one seta on its inner margin. The bud of the maxillule appears as two medial folds armed with one long seta each (Fig. 2.1).

Nauplius IV

The body length is 275 μm , and its width is 113 μm .

Nauplius IV differs from N III as follows:

The caudal margin of the hind body has added a pair of spines and a second pair of spines has been added ventrally (Fig. 2.1). The antennule consists of three segments; the second segment adds two setae on the ventral margin; three setae are added on the ventral margin and four setae to the dorsal margin of the distal segment. The anterior-most setae on the dorsal margin originate from the same notch. The setae on the inner margin of the coxa of the antenna are transformed into two long plumose setae; the basis bears three setae on its inner margin; the proximal segment of the endopod is fused to the basis and adds three setae on the inner margin; the second segment of the seven-segmented

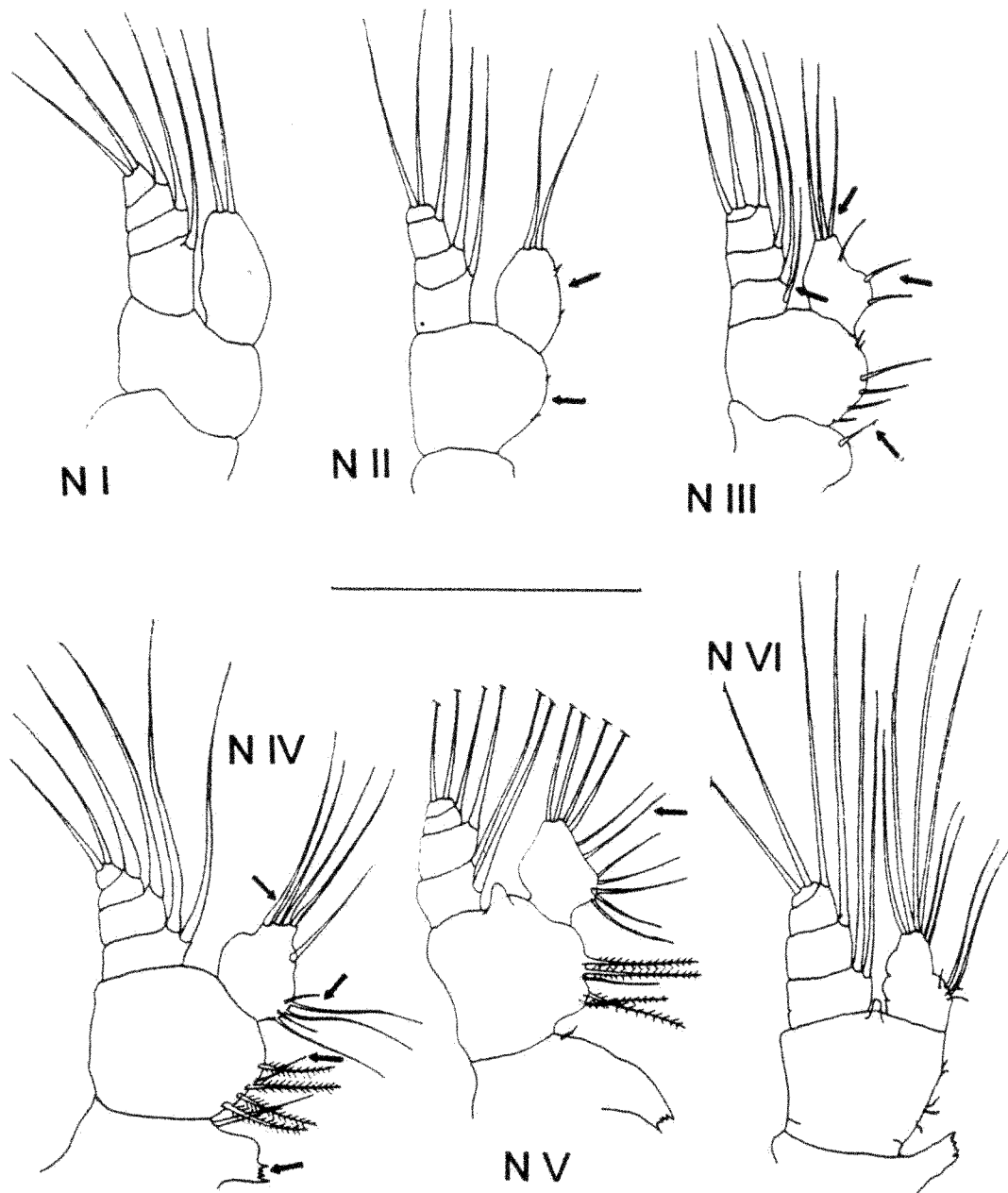


Fig. 2.4. *Metridia pacifica*. Development of naupliar mandibles in N I-VI stages. Arrows indicate new structures as compared with the preceding stage. Scale bar = 100 μm .

exopod adds two fine setae on its inner margin (Fig. 2.3). The coxa of the mandible has an endite developed as a masticatory gnathobase; the basis adds the fifth seta on its inner margin (Fig. 2.4). The endopod adds three setae grouped proximally, and one terminal seta. The maxillule is bilobed and has five setae on the endopod and three setae on the exopod (Fig. 2.5).

Nauplius V

The body length is 330 μm , and its width is 130 μm .

Nauplius V differs from N IV as follows:

The hind body adds the fourth pair of well-developed caudal spines (Fig. 2.1). The antennule is four-segmented; the distal segment is armed with two additional setae on its dorsal margin and with one additional seta on its ventral margin (Fig. 2.2). The exopod of antenna is eight-segmented, adding one segment which is armed with one long seta; the endopod is two-segmented, is separated from the basis and bears five setae terminally (Fig. 2.3). The coxa of mandible bears a small seta instead of the long coxal seta of N IV; the endopod adds one seta on its inner margin (Fig. 2.4). The exopod of the maxillule adds two setae; the endopod has four setae terminally and two slender setae laterally, while a pair of setae each are added to the two syncoxal lobes (Fig. 2.5).

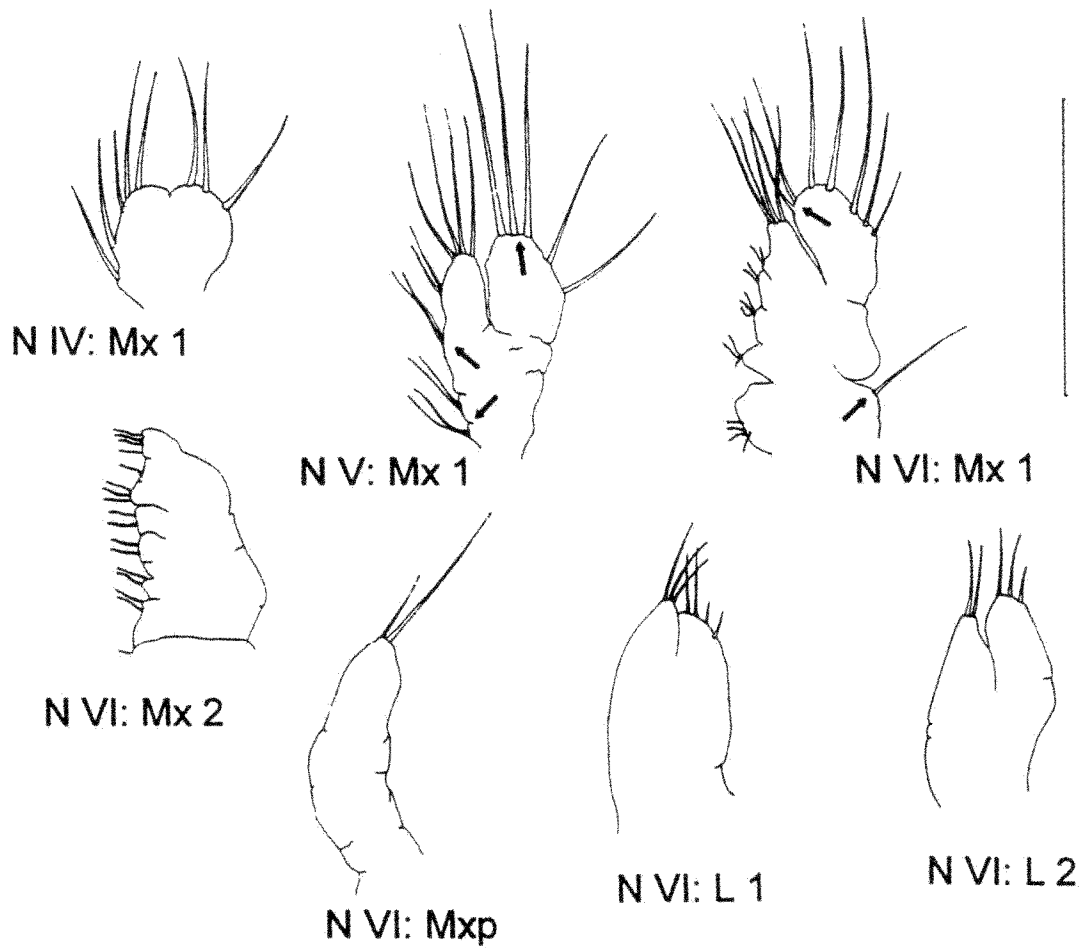


Fig. 2.5. *Metridia pacifica*. Development of naupliar maxillule (Mx I) and maxilla (Mx II), maxilliped (Mxp), swimming legs 1 (L 1), 2 (L 2). Arrows indicate new structures as compared with the preceding stage. Scale bar = 100 μm .

Nauplius VI

The body length is 385 μm , and its width is 150 μm .

Nauplius VI differs from N V as follows:

The antennule is five-segmented; its distal segment is elongate, and it adds one seta on the ventral margin and one seta on the dorsal margin (Fig. 2.2). On the inner margin of the coxa of the antenna one seta is lost, a second appears as a small spine; and both the basis and the first segment of the endopod have lost one seta on their inner margins (Fig. 2.3). The maxillular syncoxa bears long plumose setae on the outer margin; the exopod adds two slender setae; and one or two setae are added to the inner lobes of the syncoxa and basis (Fig. 2.5). The maxilla becomes uniramous with five inner lobes of syncoxa and its basis bears two setae and one seta distal to the fifth lobe. The maxilliped is elongated and bears two setae terminally (Fig. 2.5). Swimming legs 1 and 2 are present as bilobed folds (Fig. 2.5). The exopod of leg I bears two setae and two spines, and the endopod has three setae terminally. The exopod of leg II bears three setae, and the endopod is armed with two setae.

KEY TO THE NAUPLIAR STAGES OF *METRIDIA PACIFICA*

1. Nauplius bears 3 pairs of appendages.....2
- Nauplius bears more than 3 pairs of appendages.....3

- 2. Antennular distal segment has 3 setae..... N I
- Antennular distal segment has 4 setae..... N II
- 3. Maxillule precursors present as medial folds armed with 1 long seta each; hind body is armed with 2 caudal setae, 1 pair of caudal spines and 1 pair of smaller ventral spines.....N III
- Maxillule is well-developed, bears more than 1 seta; hind body is armed with 2 pairs of long ventral spines, 1 pair of denticulate caudal spines and 2 or 3 pairs of smaller lateral spines 4
- 4. Exopod of maxillule bears 3 setae; distal segment of endopod of antenna bears 4 terminal setae N IV
- Exopod of maxillule bears more than 3 setae; distal segment of endopod of antenna bears 5 terminal setae... 5
- 5. Exopod of maxillule bears 5 setae..... N V
- Exopod of maxillule bears 7 setae; nauplius bears 8 pairs of appendages; swimming leg 1 and 2 buds present as armed medial bilobed folds..... N VI

DISCUSSION

There are three other publications which provided descriptions of the naupliar stages of *Metridia* (Gibbons, 1938; Ogilvie, 1953; Lapota et al., 1988). Both Gibbons (1938) and Ogilvie (1953) described the closely-related species *Metridia lucens* from the North Atlantic. Gibbons

(1938) drew only the posterior body parts and the distal antennular segment for N IV, but gave a short written description of N I through N V. Ogilvie (1953) drew the antennules and the posterior end of the body for all six stages without further detailed descriptions.

Metridia lucens and *M. pacifica* have similar naupliar morphology (Table 2.1). There are some differences in the hind body armature at N III and in the numbers of setae on the antennular proximal segments at N I. Since the hind body of N IV-VI of both species has both larger lateral spines and smaller lateral spinules, the armature differs from the original descriptions (Table 2.1). In Table 2.1, the numbers in parentheses refer to total caudal armature including the spinules.

Lapota et al. (1988) illustrated only N IV of *Metridia longa* from the Norwegian Sea. The presence of three pairs of caudal lateral spines on the hind body and well-developed exopod and endopod of the maxillule suggests that the N V stage may have been described, but the antennule is like that of N IV of *Metridia pacifica*.

Campbell (1934) described the nauplii of *Neocalanus plumchrus* (named *Calanus tonsus*), and the comparison of those drawings with my results reveals no marked differences. It may be that the nauplii described by Campbell (1934) as "*C. tonsus*" were actually *Metridia*

Table 2.1. Differences of developmental patterns within the naupliar phase of *Metridia pacifica* (original data), *Metridia lucens* (¹ - after Gibbons (1938), ² - after Ogilvie (1953)) and *Neocalanus plumchrus* (after Campbell (1934)).

	<i>M. pacifica</i>	<i>M. lucens</i> ¹	<i>M. lucens</i> ²	<i>N. plumchrus</i>
Antennular lateral setae on 2 proximal segments at N I	absent	3	3	1
Hind body caudal armature at N II	2	2	2(4)	2
Hind body caudal armature at N III	4	n/a	4	4
Hind body caudal spines at N IV	6	6	6(8)	6(10)
Hind body caudal spines at N V	8	8	8(12)	8(10)

pacifica (Miller et al., 1984), because of the following unique characters common to stages N III-VI of Campbell's description and *M. pacifica*: the ventral spines are located a substantial distance from the caudal spines; and the two anterior-most setules on the dorsal margin of the distal segment of the antennules are very close together and originate from the same notch. Both features can be used to distinguish the nauplii of *Metridia* from those of *Calanus*, *Neocalanus* (Gibbons, 1938; Ogilvie, 1953; Batchelder, pers. comm. 01.10.1994) and *Pseudocalanus* (Ogilvie, 1953).

The size of the naupliar stages described by Campbell (1934) is much larger than that of the nauplii from both the previous works on *Metridia* and my study (Table 2.2). Campbell (1934) may have described the nauplii of *Metridia okhotensis* instead of *Neocalanus plumchrus*. *Metridia okhotensis* can be found in British Columbia waters (Gardner and Szabo, 1982). As *N. plumchrus* and *M. okhotensis* are similar in size as adults (Brodsky, 1950; Brodsky et al., 1983), it is plausible that the nauplii have similar size ranges as well. Since there is no other description of *N. plumchrus* nauplii (Sazhina, 1985, reproduced Campbell's drawings), a laboratory study of the development of *N. plumchrus* is needed.

Table 2.2. Comparative length measurements (μm) of *Metridia* nauplii (¹ - original data; ² - from Paul et al. (1996); ³ - from Gibbons (1938); ⁴ - from Ogilvie (1953)) and *Neocalanus plumchrus* (from Campbell (1934)).

Stage	<i>M. pacifica</i> ¹	<i>Metridia</i> sp. ²	<i>M. lucens</i> ³	<i>M. lucens</i> ⁴	<i>N. plumchrus</i>
N I	150-175 (n=8)	-	170-180	190	280-300
N II	175-200 (n=11)	-	210-230	210	300
N III	200-225 (n=17)	190-260	270-280	270	350
N IV	250-290 (n=8)	270-320	320-340	340	460
N V	-	350-430	400-420	410	560
N VI	-	400-500	-	460	700

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CHAPTER 3

REPRODUCTION OF *METRIDIA PACIFICA* BRODSKY (COPEPODA: CALANOIDA) AND GROWTH OF THEIR NAUPLII IN THE LABORATORY.²

ABSTRACT

The paper presents laboratory data on early life history of *Metridia pacifica* Brodsky. Clutch sizes and sperm storage potential were determined for females captured from the southeastern Bering Sea and Gulf of Alaska. None of the females produced more than one egg clutch in captivity. The mean clutch size was 12-13 eggs.d⁻¹ for females from both sites, and there was no relationship between body size and number of eggs per clutch or egg diameter. Intermolt periods for stages egg-N IV were 49-120 hours for animals reared at 3°C, and 33-69 and 27-74 hours for animals reared at 6°C and 9°C, respectively. Growth in length occurred in two slightly different phases, with N I-III, N III-V and N V-VI each having their own growth pattern. The developmental rate of

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all naupliar stages was approximated by an exponential function. The ratio of body length divided by body width considerably increased from stage N III through N IV.

INTRODUCTION

The copepod *Metridia pacifica* Brodsky, 1950 is common in subarctic Pacific and Bering Sea oceanic waters (Batchelder, 1985, 1986; Coyle et al., 1996). In the southeastern Bering Sea, the nauplii of *M. pacifica* are among the most important prey for larval walleye pollock *Theragra chalcogramma* Pallas (Hillgruber et al., 1995), one of the North Pacific's most abundant fish species (Wespestad, 1993). However, knowledge of the recruitment biology of *M. pacifica* is limited (Batchelder and Miller, 1989). Data on developmental biology, hatching time and growth rates of different stages of *M. pacifica* will improve the understanding of temporal variations in larval walleye pollock feeding success (Paul et al., 1996). This paper presents information on egg production, naupliar development and growth at different temperatures for *M. pacifica*.

METHODS

The nauplii of *M. pacifica* from the Aleutian Basin in the southeastern Bering Sea were collected in April of 1992 and 1993 and preserved for morphometric analyses (Paul et al.,

1996). Live nauplii for growth experiments were caught in the Gulf of Alaska near the town of Seward using a 0.5 m ring plankton net with 300 μm mesh. Also, live females were collected in both the southeastern Bering Sea in early May 1995 and 1996, and in Resurrection Bay near Seward in the Gulf of Alaska in fall 1995 and February 1997 (Fig. 3.1).

For the egg production experiments single females were placed into 500 ml beakers. Only those females which seemed healthy were used; individuals which swam erratically or had broken appendages were discarded. These copepods were fed excess amounts of a mixture of autotrophic flagellates (*Isochrysis galbana* and *Tetraselmis suecica*) and the diatom *Chaetoceros calcitrans* reared in pure cultures that were restarted weekly. Phytoplankton in the copepod tanks was kept at 35,500–50,000 cells.ml⁻¹ (cell counts determined by microscope). *Artemia* sp. reared for two weeks with the above flagellates were added to the mixture as animal prey for adult females because *Metridia* is omnivorous (Haq, 1967). All work was done in a constant-temperature room set at 3°C(±0.5), and incubators set at 6°C(±0.5) and 9°C(±0.6) under continuous low light (2.5–3.5 lux) or total darkness. The temperature of 3°C was selected because it is the average value observed for the upper 90 m of the water column over the Bering Sea collection site during spring (Hillgruber et al., 1995). A temperature of 6°C is typical for early spring in the Gulf of Alaska (A.J.

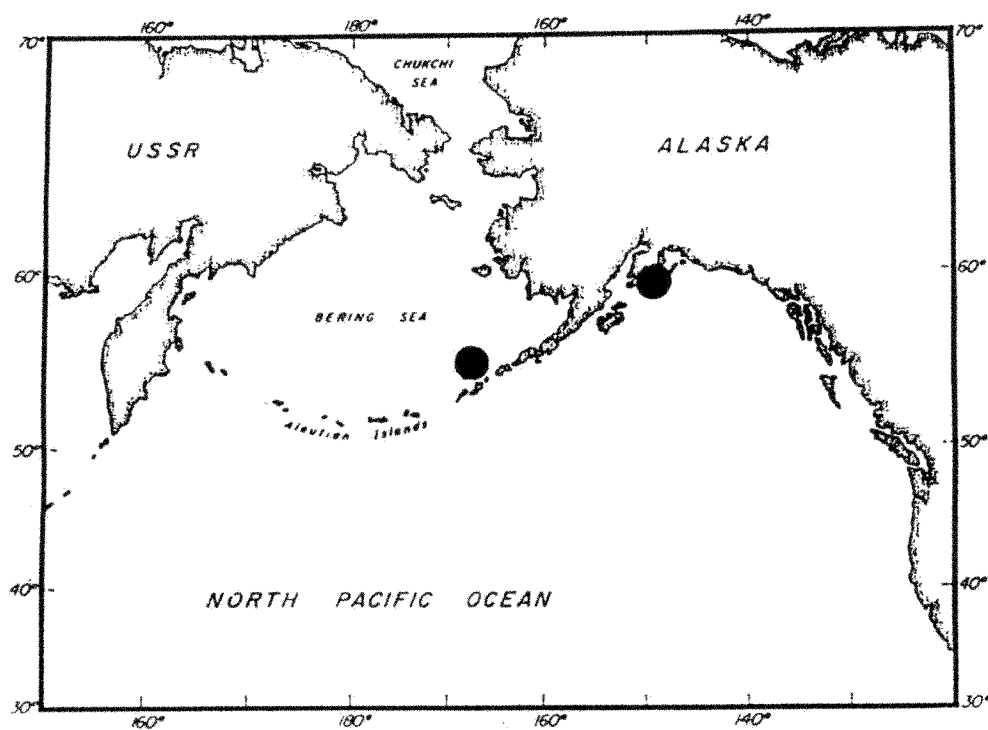


Fig. 3.1. Map shownig collection sites for *Metridia pacifica*.

Paul, unpublished), while 9°C represents the upper limit of *M. pacifica* temperature tolerance (Geletin, 1975). The contents of the beakers were examined daily under a dissection microscope and the number of new eggs and newly hatched nauplii were recorded. Periodically (1-7 days) the females were transferred to beakers with fresh seawater and food, and eggs or nauplii were removed.

For experiments on development time, a known number of eggs were placed in a 50 ml beaker. After hatching, the nauplii were pipetted to 100 ml beakers for all subsequent development. There were twenty-six experiments, each using a single clutch of eggs from different females. Ten 3°C experiments were started with eggs from females collected in May 1995 (4 females), May 1996 (5 females) and February 1997 (1 female). Four 6°C and twelve 9°C experiments were started with eggs from females caught in February 1997. Three experiments were started with naupliar stages N I-II taken from batch cultures that hatched in the fall of 1995 and four from cultures that hatched during May 1996. A census was made of the nauplii at intervals of 2 to 7 days, depending on stage, for 3°C growth studies and every 6 to 12 hours for the 6°C and 9°C observations. The data obtained from observation periods more than 4 days were not used to calculate intermolt times. On the census day, individuals were enumerated by developmental stage and transferred to beakers filled with

fresh seawater. Since both preliminary experiments and published data (Peterson, 1986) showed that high concentrations of phytoplankton increases early stage nauplii mortality, such concentrations were avoided for N I and N II non-feeding stages. After N III, when nauplii were feeding, phytoplankton was kept at ca 16,500-20,000 cells.ml⁻¹.

Since all nauplii died before molting from N IV to N V, 28 N V specimens were caught near Seward during February 1997, placed individually into 100 ml beakers and kept at 3°C. A census of the nauplii was made at 3 day intervals.

T-tests compared clutch size between the Bering Sea and Gulf of Alaska specimens, and between length of wild and laboratory reared nauplii. Paired t-tests were also used to compare stage duration relative to incubation temperature. The growth rate of N I reared at 3°C was compared to N I reared at 6°C using the t-test. Next, N I at 6°C was compared to N I at 9°C. This procedure was continued for stages N II-IV. Differences were considered significant at $P \leq 0.05$.

The total length of each individual nauplius was measured from the anterior to the posterior end excluding the caudal setae or spines. Body width was measured for the widest part of the naupliar shield. Development time is determined as time from the egg laying until molting into a specific stage, while the intermolt period is the time between two succeeding molts.

RESULTS

a) Clutch size

Only 20 females from 233 Bering Sea specimens produced eggs in captivity. The females broadcast their eggs rather than carrying them in egg-sacs. Most of the spawning occurred within 30 days of capture (Fig. 3.2). A total of 18 females of 28 Gulf of Alaska specimens broadcasted eggs and most of their spawning occurred within 8 days of isolation (Fig. 3.2). No female produced more than one egg clutch in captivity. Twelve females were held for 30 days after broadcasting eggs, and none produced additional eggs. Since females were held without males, they must be able to store sperm for at least 50 days.

The mean clutch size of Bering Sea females was 12.6 eggs (SD=8.8, range=4-35, n=12), with a mean egg diameter of 158 μm (SD=16, n=82). The mean clutch size of Gulf of Alaska specimens was 12.5 eggs (SD=5.7, range=6-26, n=15), with a mean egg diameter of 151 μm (SD=7, n=203). There were no significant differences in clutch size between the Bering Sea and Gulf of Alaska specimens. The mean daily production rate for females that extruded eggs was 12.7 eggs.individual⁻¹.day⁻¹ (SD=6.1, n=13) for Gulf of Alaska specimens. On many census days there were no eggs, indicating that females do not produce daily. Egg production by Bering Sea females was not estimated because the time between censuses was >24 hours.

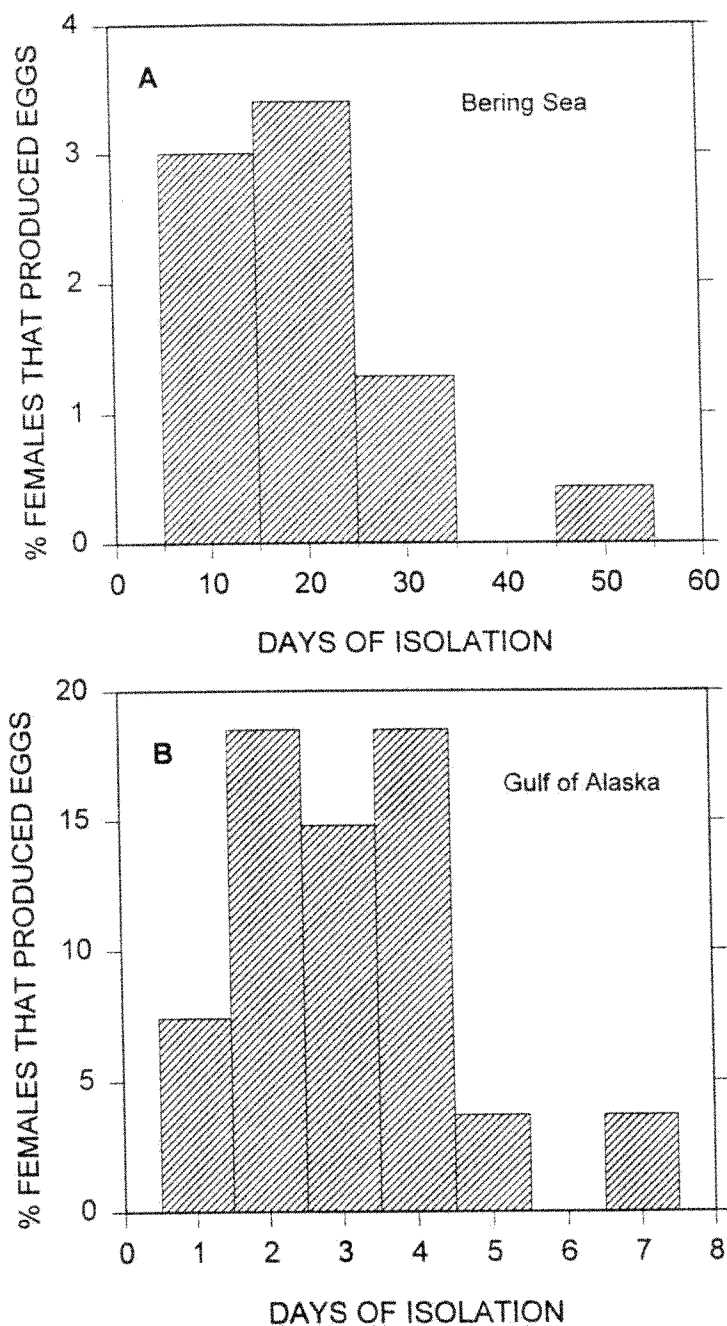


Fig. 3.2. Frequency of spawning of isolated female *Metridia pacifica* relying on stored sperm to fertilize the clutch. These females were collected from the Bering Sea (A) and Gulf of Alaska (B) and maintained in the laboratory at 3°C.

There was no obvious effect of body size on number of eggs per clutch nor average egg diameter (Fig. 3.3).

b) Development

Estimates of the stage duration of eggs and nauplii ranged from 27 hours (N I, 9°C) to 70 hours (N III, 3°C) (Table 3.1). Most eggs hatched within 6 hours of each other. Despite numerous attempts we were unsuccessful in rearing nauplii further than N IV. The growth data for stage N VI at 3°C were obtained from experiments with wild Gulf of Alaska nauplii. The overall pattern of development from N I to N IV at 3°C was a linear function with a slope of $83.5 \text{ h.stage}^{-1}$ (Fig. 3.4). Stage durations were significantly different for all stages and temperatures. In all cases the P value was ≤ 0.05 . The pattern seemed to be rapid development for stages N I-II and slower development for N III-IV (Fig. 3.4). Development times for each stage at 6°C and 9°C were faster than those at 3°C, and the overall pattern of development was not linear (Fig. 3.4). This trend is consistent with the ratio of body length divided by body width for the different stages (Fig. 3.5). This ratio increased from stage N III through N IV. The development time from egg to N III was 312 hours at 3°C and 184 hours at 9°C (Fig. 3.6).

c) Growth

Table 3.1. Duration of egg and naupliar stages of Metridia pacifica reared in the laboratory.

Stage	Hours (Mean/SD/Range)			
	3°C	3°C	6°C	9°C
	Bering Sea	Gulf of Alaska	Gulf of Alaska	Gulf of Alaska
	specimens	specimens	specimens	specimens
Egg	53/12/24-72 (n=89)	56/0/0 (n=9)	46/5/43-53 (n=48)	35/6/27-42 (n=130)
N I	49/3/14 (n=14)	52/0/0 (n=9)	33/2/32-36 (n=48)	27/4/24-32 (n=75)
N II	90/10/72-96 (n=33)	70/0/0 (n=9)	60/6/51-68 (n=48)	48/7/38-59 (n=90)
N III	-	120/0/0	69/1/68-70 (n=33)	74/4/72-83 (n=24)
N VI	-	180/0/0 (n=3)	-	-

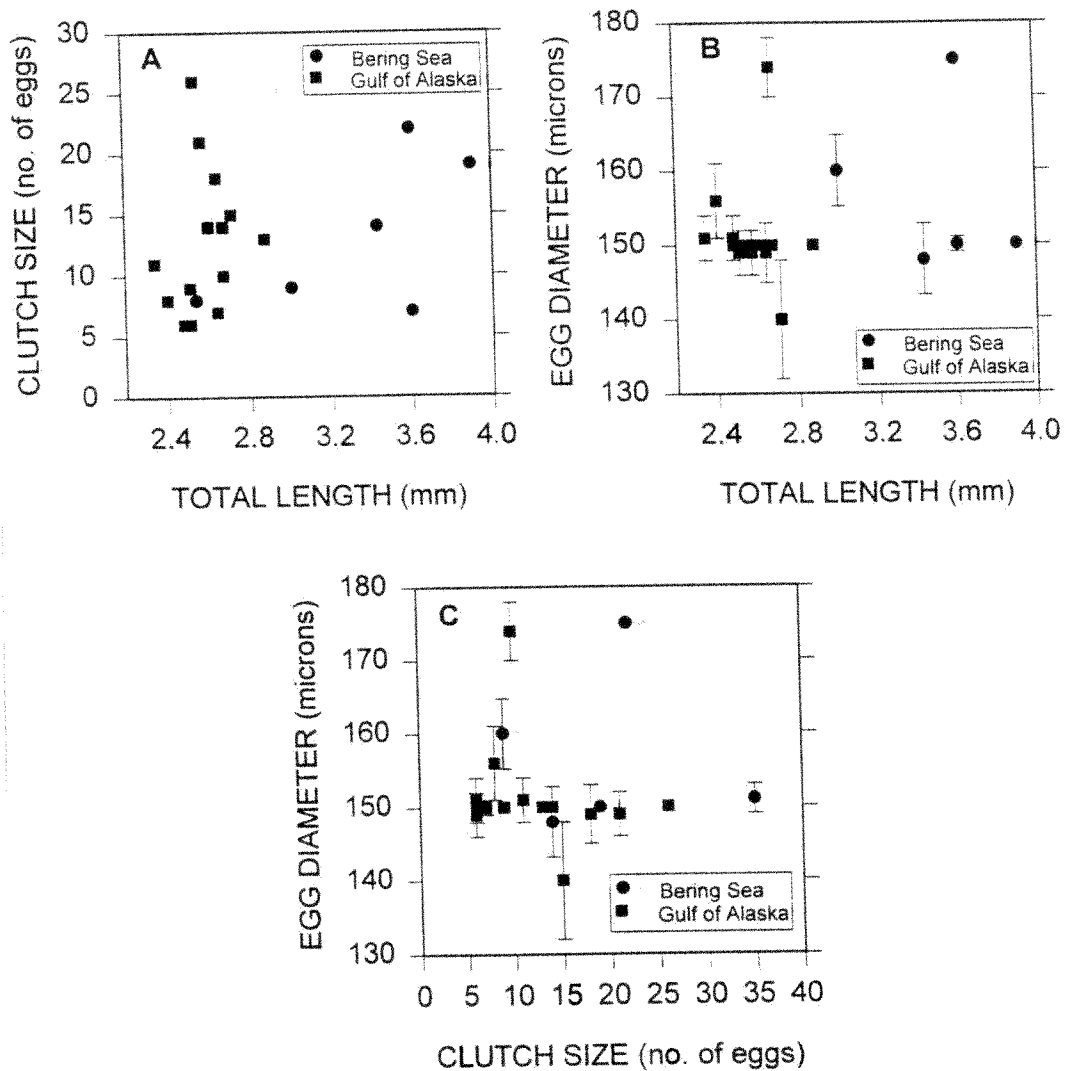


Fig. 3.3. The relationship between the size of *Metridia pacifica* and their eggs. A - female total length (TL) vs. clutch size; B - TL vs. average egg diameter (vertical bars = SD); C - clutch size vs. average egg diameter (vertical bars = SD).

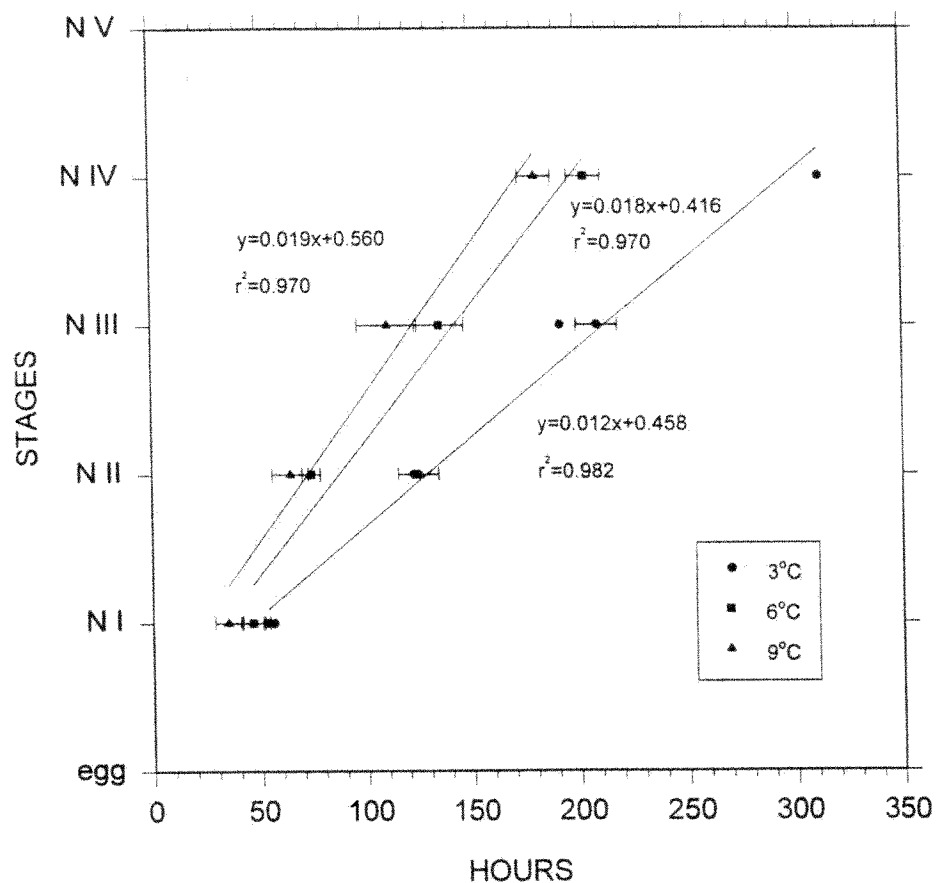


Fig. 3.4. Development rates for *Metridia pacifica* naupliar stages N I-IV reared at 3°C, 6°C and 9°C. Symbols are the average times when individuals just entered a stage (horizontal bars = SD).

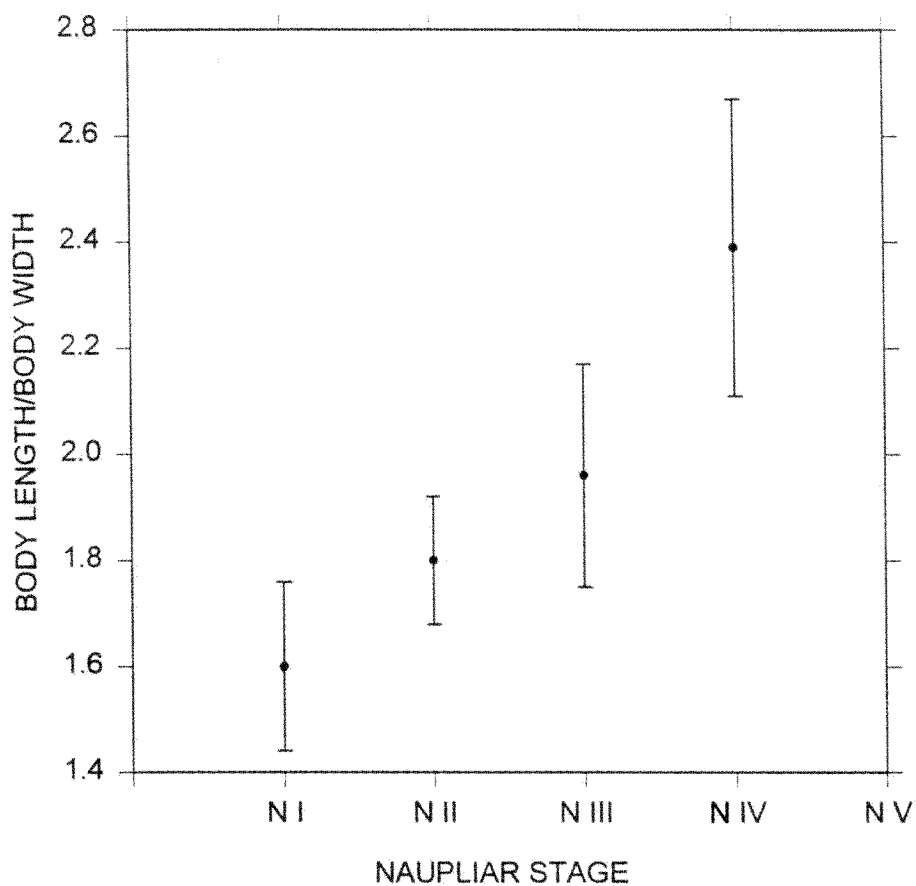


Fig. 3.5. The ratio of body length divided by body width for the naupliar stages of *Metridia pacifica*.

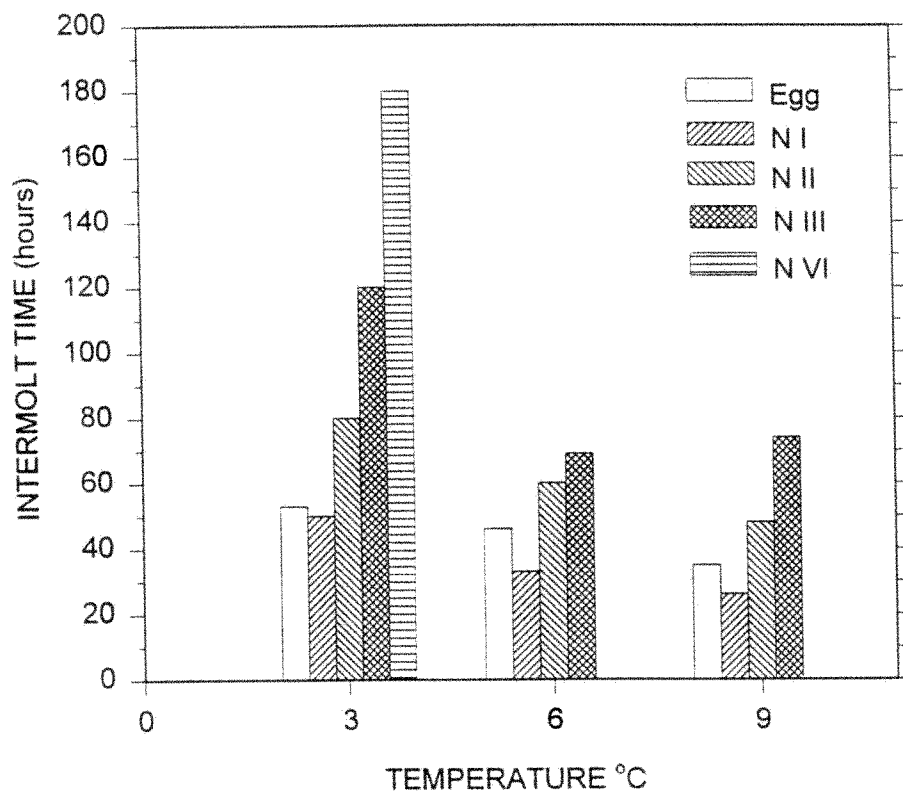


Fig. 3.6. Duration of the intermolt periods for *Metridia pacifica* naupliar stages N I-III and N VI reared at 3°C, 6°C and 9°C.

The relation between body length and stage for *M. pacifica*, based on both laboratory-reared and field-caught specimens, shows that change in length with stage occurred in 3 linear phases (Fig. 3.7). First, N I to N III; second, N III to N V, and third, N V to N VI. The body length measurements of wild nauplii of N III and N IV did not significantly differ from those of laboratory reared specimens. These results suggest that the laboratory conditions under which the copepods were raised did not alter the relationship between stage and size.

The changes of body length (microns) with time (hours) from stage N I through N IV were non-linear, longer in duration from N III to N IV, with a bigger increase in body length. However, logarithmically transformed data was approximated by a linear function (Fig. 3.8).

DISCUSSION

Metridia pacifica undergoes strong diel vertical migrations (Vinogradov, 1968; Batchelder, 1985; Hattori, 1989). Nauplii can be found at 500 m depth, while they are most numerous in the upper 100 m layer (Batchelder, 1985). Perhaps the lack of a chance to move vertically in captivity caused stress that resulted in the deaths of older nauplii. Little is known about the diets of *Metridia* spp., especially

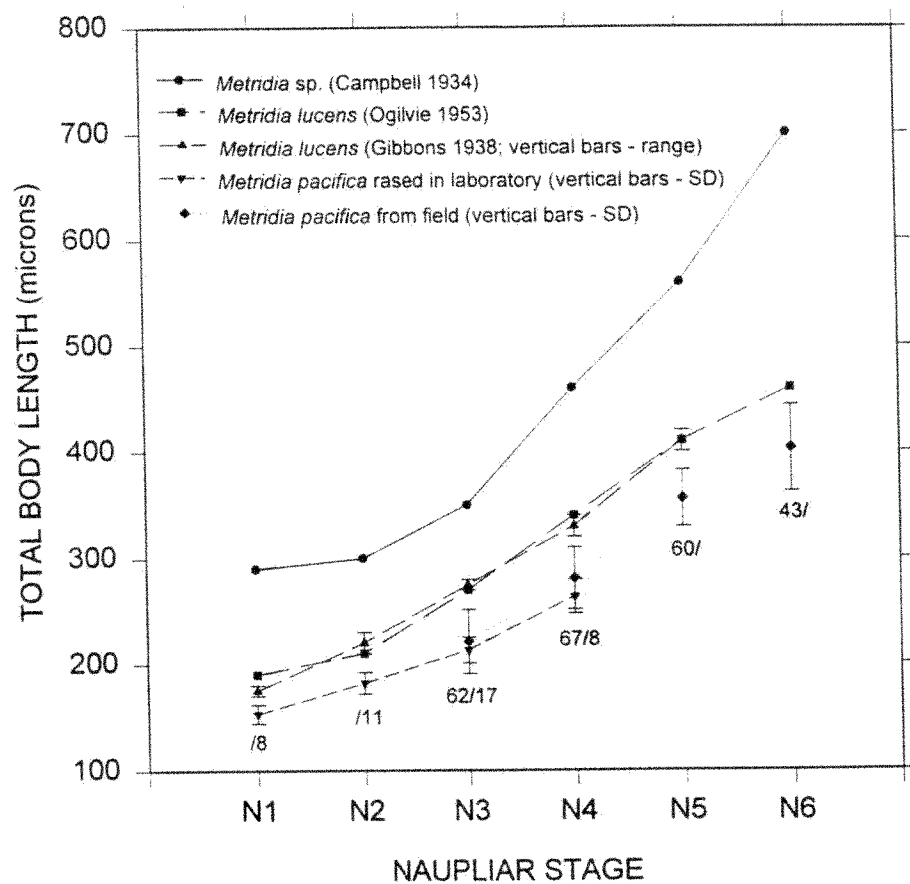


Fig. 3.7. Comparison of average naupliar body length changes in different *Metridia* species.

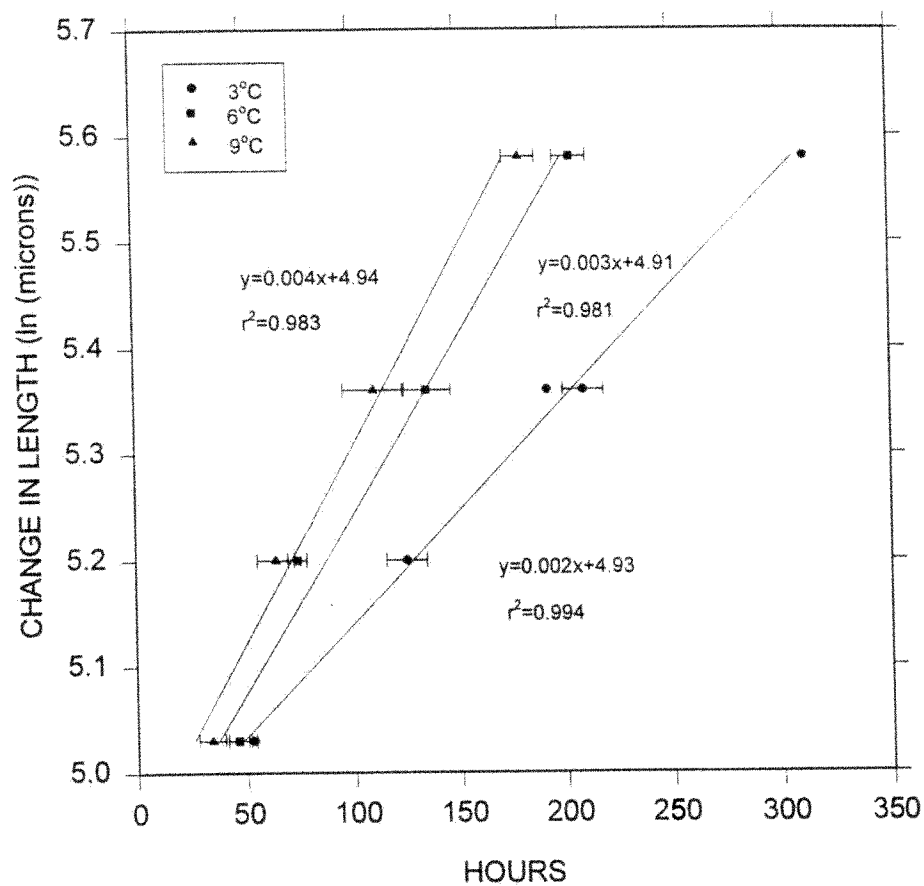


Fig. 3.8. Length growth of *Metridia pacifica* naupliar stages N I-IV reared at 3°C, 6°C and 9°C. Data on body length are logarithmically transformed.

the naupliar stages. It could be that some bacteria or heterotrophic protozoans are important food for the older nauplii (Roff et al., 1995) and our diet was deficient in some way.

In Figure 3.4 individuals from both the Bering Sea and Gulf of Alaska were included in the temperature growth rate experiments. It is possible that individuals from these two regions might grow at different rates relative to the rearing temperature resulting from their adaptations to different thermal conditions in the Bering Sea and Gulf of Alaska. At this time there is not enough information to test this possibility.

The Alaska Coastal Current may contribute Gulf of Alaska copepods to southeastern Bering Sea populations (Coachman, 1982). Thus, there may not be profound genetic differences in the development rates of southeastern Bering Sea and Gulf of Alaska *M. pacifica* relative to temperature. In the future, experiments measuring growth rates of Gulf of Alaska and Bering Sea *M. pacifica* nauplii will have to be completed separately to answer these questions. Individuals were also hatched during different months and this may confound the experimental results.

It has been reported that for marine copepods the growth rate may change from stage to stage (Paffenhöffer and Harris, 1976; Klein-Breteler et al., 1982; Kimoto et al., 1986;

Peterson, 1986). The pattern of early development of *M. pacifica* largely conforms to previously described patterns (Landry, 1983; Peterson, 1986). It features the relatively short duration of the pre-feeding NI-II and longer duration thereafter. Landry (1983) suggested that the first two naupliar stages are of short duration because they do not feed and that N III is longer because it needs to recover the weight lost during the two non-feeding stages. However, the overall copepod development pattern, with the possible exception of copepodid stage V for some species, is generally approximated by a linear function (Miller et al., 1977, Landry, 1983, Peterson, 1986, Sabatini and Kiorboe, 1994) like that observed for *M. pacifica*.

The comparison of our stage vs. length measurements with other studies shows that the development patterns of *M. pacifica* and *M. lucens* are similar. *Metridia* sp. described by Campbell (1934) from the North Pacific but mis-identified as *N. plumchrus* (Pinchuk, 1997) are also similar (Fig. 3.7). It has been suggested that despite some differences in thermally related specific growth rates "an exponential model provides the best general approximation of the growth of marine copepods over the entire life cycle from egg to adult" (Huntley and Lopez, 1992). Vidal and Smith (1986) used an exponential growth model to estimate the production of *Eucalanus bungii* and *M. pacifica* in the Bering Sea. Our growth

data for most stages of *M. pacifica* seem to be consistent with that assumption.

Both development time and length-growth approximations can be used to estimate duration of various phases of *Metridia* life history (Figs. 3.4, 3.8). Walleye pollock larvae select for N IV-N VI *Metridia* nauplii and seldom eat the younger stages (Hillgruber et al., 1995). Based on our growth rate studies at 3°C it takes about 12 days for *M. pacifica* to develop from egg to N IV; at 6°C it takes 8 days.

At 3°C it would take about 40 days to grow from egg to adult, if the growth pattern (Fig. 3.4) remains constant for the older nauplii and copepodids. The generation time for adult *M. pacifica* of 2.4 to 3.6 mm length at 3°C would be 56-65 days from the length growth model (Fig. 3.8). Vidal and Smith (1986), using cohort analysis, estimated *M. pacifica* generation time in the southeastern Bering Sea in spring as 50-55 days assuming the copepodid phase takes 30-35 days. Our results demonstrate that the naupliar phase takes 23-30 days and thus the laboratory growth rate measurements appear to approximate *M. pacifica* growth *in vivo*.

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CHAPTER 4

DISCUSSION

TAXONOMIC CLARIFICATION

The taxonomic status of *Metridia pacifica* Brodsky remains unclear. Originally it was described (Brodsky, 1950) as the North Pacific sibling species to North Atlantic *Metridia lucens* (Boeck, 1864). Previously the species has been identified as *M. lucens*, but many authors noted differences (Giesbrecht, 1895; Esterly, 1924; Stepanova, 1937; Brodsky, 1941). The major distinctive features of the new species were the steeper cephalothorax, the longer inner seta on the distal segment of the female fifth swimming leg, and the presence of a spine on the inner margin of the third segment of the male left fifth swimming leg (Brodsky, 1950). Brodsky (1950) noted that there was significant variety in the last two characters, and cephalothorax shape remained the most distinctive feature. It was supposed that the two species were geographically isolated from each other (Brodsky, 1950).

Some authors suggested that *M. pacifica* and *M. lucens* are taxonomically identical (Park, 1968; Beklemishev, 1969, Bollens et al., 1993, Osgood and Frost, 1994), while a recent DNA study defined *M. pacifica* and *M. lucens* as different (Bucklin et al., 1995). Others assumed that both species can co-occur in the North Pacific (Gardner and Szabo, 1982).

Geletin (1975) distinguished two *Metridia* forms by matching characters of these species from the Western North Pacific and proposed that they both be called *M. pacifica* until a detailed comparative morphological study is done.

Whereas a few specimens sharing *M. lucens* features were found in Gulf of Alaska in September 1996 (A. Pinchuk, personal observation), only copepods matching the characters of *M. pacifica* were used for this study.

ECOLOGICAL IMPLIFICATIONS

The growth of non-feeding stages N I-N III is presumably temperature dependent, since they do not eat (Sazhina, 1985). Their linear growth matches an exponential model, which is considered the best general approximation of overall growth patterns for all marine copepods raised in excess food (Huntley and Lopez, 1992). In terms of recruitment, the progression of developmental stages through time follows patterns similar to those of other marine copepods. Furthermore, results of a cohort analysis for the *M. pacifica* population in the southeastern Bering Sea yield similar estimates of generation times for naupliar and copepodid phases (Vidal and Smith, 1986). Thus, the temperature-dependent, exponential growth model should be applicable to calculating the production of *M. pacifica* populations

regardless of their locations, provided the animals are food satiated (McLaren, 1978).

McLaren (1978) concluded that trophodynamic studies would not contribute significantly to estimating secondary production. Huntley and Boyd (1984) reported that although the growth of zooplankton in oceanic regions must often be food-limited, zooplankton in coastal waters are not. Huntley and Lopez (1992) analyzed numerous reports and hypothesized that in the ocean, copepods always seem to be able to find sufficient food to grow at maximal rates, even when measured food concentrations are low. Measuring phytoplankton availability is problematic due to its spatial and temporal patchiness, but copepods can exploit these patches by moving vertically to find them. The similarity of generation time estimates obtained using cohort analysis (Vidal and Smith, 1986) and my physiological method supports this assumption.

Growth rates of first feeding pollock larvae are dependent on the availability of copepod nauplii (Haldorson et al., 1989). The data on egg production, growth and development of *M. pacifica*, together with field population data, can be used to estimate the rate at which the nauplii of *M. pacifica* will grow to the size and stages utilized by walleye pollock larvae.

CONCLUSIONS.

The conclusions from my research are:

1. Ontogenetic morphological changes of the nauplii of cultured *M. pacifica* are similar to those of *M. lucens*, but some minor differences do exist. The published description of *Neocalanus plumchrus* nauplii is identical to that of *Metridia pacifica*, except for size.
2. Clutch size and egg diameters do not depend on female body size.
3. Developmental rates of naupliar stages are describable by a linear function, which can be used to estimate recruitment schedules for nauplii at given temperatures.
4. Growth in length follows an exponential model, and is approximated by a linear function on a logarithmic scale.

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